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The influence of bottom type and shelf position on biodiversity of tropical fish inside a recently enlarged marine reserve

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ABSTRACT

1. A necessary component of implementing a successful marine reserve is the quantification of the biological resources that fall under its protection. Without such an initial assessment, the future effects of the reserve on the local habitat and biotic community cannot be quantified and will remain the subject of debate.

2. This study provides such a baseline assessment of fish diversity and habitat types within a recently enlarged marine reserve. Buck Island Reef National Monument, US Virgin Islands, was recently enlarged from approximately 4 km^2 to over 76 km^2. Areas of sand, seagrass, and hard-bottom under protection were increased from 0.29 km^2, 0.47 km^2, and 1.96 km^2 to 2.70 km^2, 2.89 km^2, and 18.30 km^2 respectively when the Monument was expanded. A 53 km^2 area of pelagic/deep-water habitat with unknown bottom type is now also protected by the Monument.

3. Visual counts of fish within $25 \times 4\,m^2$ transects conducted during the day were used to assess fish community structure and habitat utilization patterns. Species richness, diversity, assemblage structure, and fish density were evaluated and compared among sand, seagrass, and hard-bottom habitats. Hard-bottom sites had over twice the mean species richness and diversity as sand and seagrass sites, and several times greater mean fish density.

4. Quantification of the fish community in pelagic and deep-water habitats within the reserve is recommended to provide a more comprehensive assessment of the offshore areas of the reserve. Fish numbers, size, and diversity outside the reserve boundaries must also be evaluated to allow quantification of the effects of the marine reserve on the adjacent fish communities.

KEY WORDS: reef fish; coral ecosystem; biodiversity; marine reserve; baseline; inventory

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INTRODUCTION

Coral reef ecosystems have long been recognized as focal points of marine biodiversity (Sebens, 1994; Reaka-Kudla, 1996). Protecting this diversity through such mechanisms as marine reserves has been identified as an important goal by many academic and governmental groups (Ehrlich and Wilson, 1991; Meffe and Carroll, 1997; Executive Order 13089, 1998). However, rigorous quantification, at appropriate spatial and temporal scales, of the flora and fauna of protected reef ecosystems by reserves has been only patchy at best (Jackson, 1991; Jackson *et al.*, 2001; Rogers and Beets, 2001). Biological inventories of reef ecosystems not protected by reserves are even more uncommon. Dramatic alterations to community structure and biodiversity of Caribbean reef ecosystems are suspected to have taken place over the last two centuries primarily due to fishing, although specific trends over this time-scale have generally gone unquantified (Jackson, 1997). This lack of quantitative characterization leads to a 'shifting baseline' attitude in which successive generations discount older anecdotal accounts of high fish abundance as simple exaggerations (Pauly, 1995). If no quantitative historical information is available upon which to base expectations of fishery resources, then each generation acclimates to its current condition. The result is a long-term, unrecognized decline in resources.

Fisheries often impact various components of the fish community to different degrees. Gear such as fish traps with specific mesh dimensions preferentially harvest larger fish that use structural refuges (Sary *et al.*, 1997; Wolff *et al.*, 1999). Other practices, such as hook and line fishing, preferentially target specific feeding guilds (e.g. piscivores) and size classes (Ralston, 1990; Friedlander and DeMartini, 2002). The cumulative effect of hundreds of years of selective exploitation of fish communities has resulted in significant alterations to the natural fish assemblage and trophic ecology of most coral ecosystems (Jackson, 1997; Rogers and Beets, 2001; Friedlander and DeMartini, 2002).

Marine reserves, or more specifically no-take areas, have received much attention in recent years as potential management tools to mitigate fisheries impacts on tropical marine species and ecosystems (Dugan and Davis, 1993; Dayton *et al.*, 2000; National Research Council, 2001). By removing the effects of fishing pressure and the changes in community structure that result from fishery selection, the fish assemblage within the reserve functions as a more natural system, which allows for a better understanding of the natural environmental and biotic influences that shape the biodiversity of fish assemblages (Randall, 1982; Sebens, 1994). The reserve functions as a buffer against uncertainty in conventional management techniques and as a source of recruits and ecosystem stability (National Research Council, 2001). A necessary component of implementing a successful reserve is the quantification of the biological resources that fall under its protection (Dayton *et al.*, 2000). Without baseline metrics, the intended effects of the reserve on the biotic community cannot be effectively monitored and the reserve's ultimate value in the context of nearby ecosystems fails to be quantified.

In addition to fisheries impacts, major changes have occurred in Caribbean reef ecosystems over the last several decades due to coral and invertebrate diseases that have decimated once common species such as elkhorn coral, *Acropora palmata* (Gladfelter, 1982), and the black sea urchin, *Diadema antillarim* (Lessons *et al.*, 1984). These ecosystem changes have, in turn, influenced fish community structure through a variety of ecological pathways (Rogers and Beets, 2001). Unfortunately, studies of the resulting changes in the fish community have been hampered by a general lack of baseline characterization of assemblage structure in affected areas.

The objective of this study is to provide a baseline assessment of the fish communities within the Buck Island Reef National Monument (BIRNM), US Virgin Islands (Figure 1). The BIRNM was originally designated as a marine protected area by the US Department of Interior in 1961 (Presidential Proclamation 3443, 1962). The Monument includes a small, 0.7 km^2 island north east of St Croix. Originally, the Monument included only this island and its fringing reef, which forms a shallow lagoon with typical depths ranging between 1 and 5 m. The BIRNM's boundaries were subsequently modified slightly in 1975

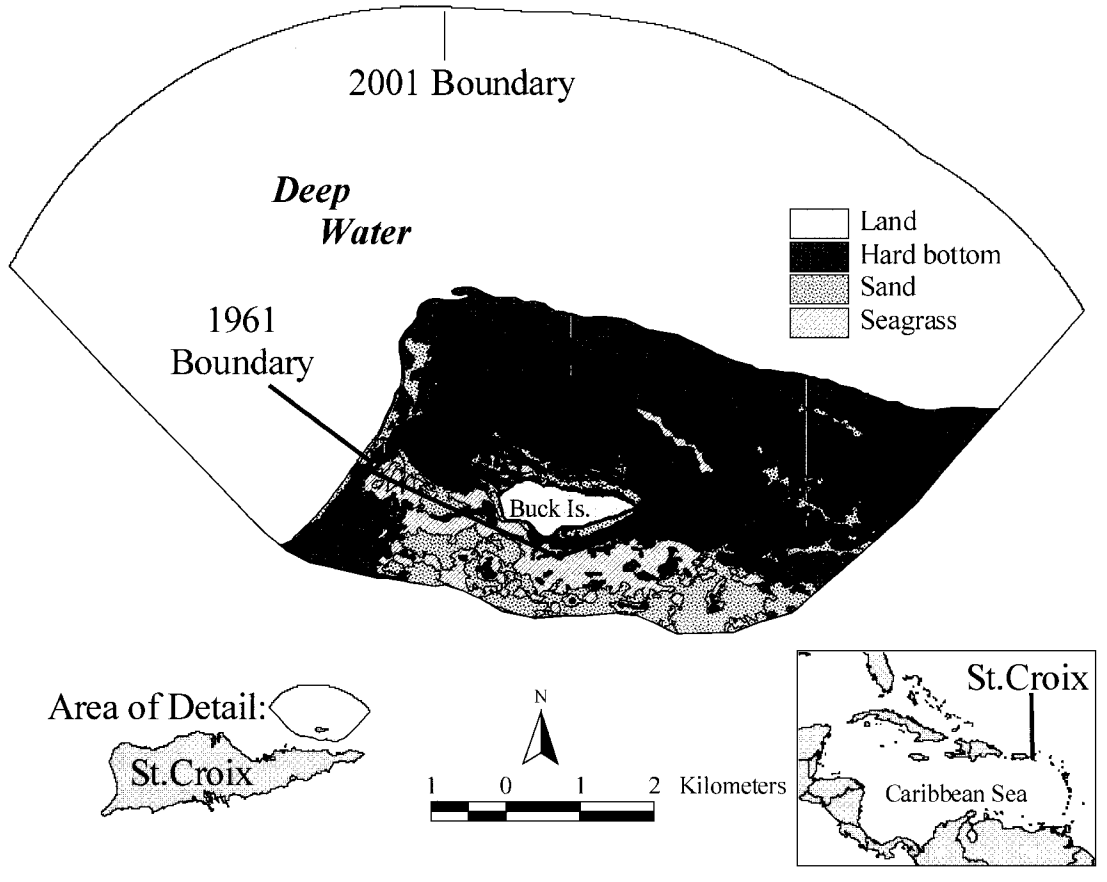

Figure 1. Buck Island Reef National Monument, St Croix, US Virgin Islands. Park boundaries from 1961 and 2001 are noted, along with habitats delineated from aerial photography. Solid grey areas denote hard-bottom, striped areas are seagrass, and stippled areas are sand.

(Presidential Proclamation 4346, 1975) and then extensively expanded in 2001 (Presidential Proclamation 7392, 2001). With this boundary enlargement, the BIRNM now includes approximately 76 km^2 of beaches, coral reefs, seagrass beds, and other benthic features seaward of the fringing reef. This bank area has typical depths ranging from 10 to 20 m before dropping off the insular shelf into deep oceanic water. Historically, net, spear, and trap fishing have occurred throughout the Monument despite the presence of a small no-take area selected at the time of the 1961 designation. With the expansion of the BIRNM's boundaries in 2001, all extractive uses, including all forms of fishing, have been prohibited throughout the Monument.

Prior to this assessment, few surveys of fish community structure had been conducted in the area, and those surveys were limited in scope to single habitat types in small areas within the BIRNM (Simpson, 1979). This study provides a baseline assessment of fish biodiversity for a variety of habitats within the newly expanded marine protected area and will also quantify the gains in habitat area and biodiversity that resulted from enlargement of the BIRNM's boundaries. The specific objectives of this study were:

1. To quantify the areas of the major bottom types and reef zones within the BIRNM boundaries pre- and post-reserve expansion.

2. To provide a baseline characterization of the fish community within the new BIRNM boundaries against which future measurements of assemblage structure can be compared to determine the effectiveness of the reserve. A related goal is to identify the species present in the fish communities that are associated with the main bottom types (sand, seagrass, and hard-bottom) in the old and new BIRNM boundaries and within each of two reef zones (lagoon and bank/shelf).
3. To derive estimates of fish density from census data and apply those values to the habitat area measurements obtained from objective 1. This will allow rough quantification of the abundance of fish within the old and new BIRNM boundaries for comparison against future assessments.

METHODS

Calculations of habitat area within BIRNM and the selection of fish census locations were based on recently completed benthic maps of the US Virgin Islands (Kendall *et al.*, 2001; NOAA, 2001). In these maps, benthic features were delineated through visual interpretation of aerial photography and assigned two attributes: (1) substrate or benthic cover type (sand, seagrass, and hard-bottom); and (2) location on the insular shelf relative to the fringing reef around Buck Island (inside the lagoon versus outside on the bank/shelf). This thematic classification of the maps allowed six spatial strata (three bottom types by two zones) to be constructed for use in selecting fish census locations across a representative range of habitats within the old and new BIRNM boundaries. The area of each of the major bottom types was calculated within both the old and new BIRNM boundaries.

A belt transect technique during which fish are visually censused was selected as the optimal method to characterize the fish communities in the BIRNM, given the complexity and variety of the habitats in the area and the need to affect fish minimally within the park. The visual transect technique provides the single most thorough and least time-consuming assessment of fish biodiversity, allowing fish at a large number of locations to be censused quantitatively (Sanderson and Solonsky, 1986). It is important to note, however, that the abundance and diversity of cryptic species and those concealed inside the reef or burrowed in sediment are a significant component of the diversity of reef fish communities, but they are underestimated with this technique (Brock, 1982). Unfortunately, those species can only be sampled with more destructive techniques, such as breaking reef substrate apart to expose cryptic fish or the use of ichthyocides to render them immobile. Since these techniques are more time consuming, under-sample active or mobile species, and are generally harmful to reef fauna, we chose to use the visual transect, which allowed for very efficient identification and quantification of the overall fish assemblage (Sale and Douglas, 1981; Sanderson and Solonsky, 1986).

This assessment includes multiple metrics to consider not only generalized changes to biodiversity and fish community structure, such as species richness and diversity, but also techniques that consider the trophic ratios and component species of assemblages associated with particular strata. Since no single metric of community structure can simultaneously describe all aspects of biodiversity that are of interest for evaluating fish assemblages, a suite of measures that each compartmentalize different components of community structure is required. These include such metrics as species richness and diversity, and multivariate approaches, such as clustering and principal components (Kaufman and Ebersole, 1984; Alevizon *et al.*, 1985; McGehee, 1994).

Although multiple metrics were used to evaluate biodiversity, as noted above, species richness was used as the metric for selecting the numbers of transects within strata, since one of the main objectives of the assessment was to determine which species are present within habitat strata. We used rarefaction of species richness from historical fish survey data from the study area to determine the number of surveys needed. The only data available for BIRNM consisted of point counts over the fringing reefs at the east end of the island conducted between 1989 and 1993 (Hillis-Starr, pers. comm.). Rarefaction of these data indicated

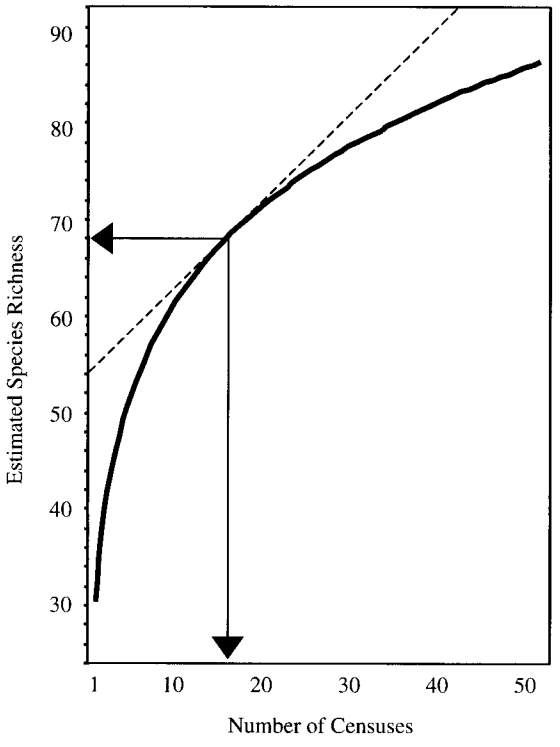

Figure 2. Rarefaction of species richness from historical fish survey data of the BIRNM. The plot is based on data from point counts conducted from 1989 to 1993 over the fringing reefs at the east end of the island. To the left of the vertical arrow, additional species are encountered at a rate of greater than one per dive. To the right of the vertical arrow, more species are encountered at a rate of less than one per dive, with this rate declining asymptotically on additional dives. The dotted line denotes the slope of a line with a one-for-one increase in cumulative species richness per survey.

that the first census in a reef area would result in observation of approximately 30 species (Figure 2). Additional species would be encountered at a rate of greater than one per census until 16 censuses are performed. Sixteen surveys in the high-diversity reef strata would result in a cumulative richness of 69 species. On additional surveys, more species would be encountered at a rate of less than one per census with this rate declining continually on additional dives. Using 16 censuses as a starting point, the desired number of surveys per stratum was increased to 24 sites to census as many species as possible to a point where additional sampling effort reached unacceptably low return in cumulative species found. The number of census sites selected was also 24 because: (1) we were sampling new strata with unknown diversity; (2) changes in biodiversity may have occurred since the time the historical surveys were conducted; and (3) the transect technique we used was likely to include a different number of species than the point counts that were the basis of the rarefaction.

Twenty-four sites were randomly selected as census locations within each of the following strata: bank/shelf:sand, bank/shelf:seagrass, bank/shelf:hard-bottom, and lagoon:hard-bottom. Only 12 sites were randomly selected from lagoon:sand and lagoon:seagrass strata because preliminary census data revealed that these locations had fewer species and individuals. This resulted in a total of 120 census locations for which the spatial coordinates were uploaded into global positioning system (GPS) units to allow easy navigation to census sites in the field. All field work was conducted during February 2001.

Once at a given census site a diver secured one end of a 25 m tape reel to the substrate. The diver then swam along a randomly selected compass heading until the tape was completely unreeled. While swimming,

the diver recorded all fish observed within 2 m of both sides of the transect to the lowest possible taxon, their abundance, and estimated fork length within 5 cm size classes up to 35 cm. For individual fish over 35 cm fork length, size was estimated visually. Swimming speed was maintained such that the $25 \times 4\,m^2$ transect ($100\,m^2$) was completed in approximately 15 min regardless of substrate type or complexity. At this slow speed, all habitat types, including complex reefs, are thoroughly censused. Performing all $100\,m^2$ transects for the same duration resulted in standardization of both area and survey time, which allowed easy comparisons among strata. It was also important to standardize transect duration to give pelagic fish the same temporal opportunity to be sampled regardless of the substrate complexity. All surveys were conducted during the day.

Mean number of fish per $100\,m^2$ survey and sighting frequency of each species were calculated for all surveys, zones, structures, and each of the spatial strata. Sighting frequency was calculated as the percentage of surveys in a given stratum in which the species was present. Next, mean fish density, mean species richness, and mean diversity were calculated for each of the spatial strata. Mean fish density is simply the total number of individuals of all species within a transect divided by the $100\,m^2$ area surveyed. This value was used in conjunction with tabulations of different habitat acreages in the Monument to estimate the total population of fish within the BIRNM. Species richness was calculated as the mean number of species observed on surveys within each stratum to allow comparisons of relative richness among strata. Absolute species richness is also provided for comparing the number of species present between the old and new BIRNM boundaries. The Shannon index H' (Shannon and Weaver, 1949), was used to calculate diversity for each survey as follows:

$$H' = -\left(\sum_{i=1}^{S} \frac{n_i}{N} \log \frac{n_i}{N}\right)$$

where S is the number of species; n_i is the abundance of the ith species and N is the total abundance of all species.

To understand the trophic diversity of each stratum, species were assigned to one of seven trophic groups based on primary feeding mode. These feeding guilds were assigned based on published gut-content studies (e.g. Randall, 1967, 1996) and personal observations. Trophic groups were piscivore (P), herbivore (H), omnivore (O; fish and/or invertebrates present in gut as well as non-incidental vegetation), zooplanktivore (Z), fish that feed on sessile invertebrates (SI), fish that feed on mobile invertebrates (MI), and fish that feed on mobile invertebrates as well as other fish (MI/P) (Randall, 1996).

The ratio of fish in each of the feeding guilds was calculated as the mean number of individuals within each trophic group converted to the percentage of total fish in that stratum. The trophic structure of each stratum was examined by plotting the relative abundance of fish in each feeding guild. Ratios, rather than absolute numbers, were examined to facilitate comparison of trophic structure among strata.

Density, richness, and diversity values did not conform to the assumptions of parametric analysis and could not be transformed to do so. Therefore, non-parametric approaches were used to determine whether species density, richness, and diversity differed significantly among the six spatial strata. First, a Kruskal–Wallis test was used to evaluate these variables among all strata to determine if pairwise tests were warranted. When significance was found, a non-parametric, Tukey-type multiple-means comparison test was conducted to determine which strata differed (Zar, 1999). Interquartile range is presented in the results rather than the means and standard error of the mean, since non-parametric analyses were used to detect differences among strata.

Hierarchical clustering was used to evaluate the similarity of species assemblages among strata. First, each of the 103 species observed was scored as present or absent at each site. Next, the proportion of surveys on which a given species was found was calculated for each stratum. Ward's minimum variance

method was used to cluster strata based on these sighting frequencies for all 103 species. Strata with similar species membership cluster closer together than strata that share fewer species.

Principal components analysis (PCA) was also used to explore the associations among specific taxa and spatial strata. Similar to the cluster analysis, PCA was based on frequency of occurrence of each species within each stratum.

Fish densities were used in conjunction with the habitat maps to estimate the total fish population of the Monument before and after boundary expansion. Because the bottom type was the primary determinant of fish density rather than the zone, the population size calculations were based on fish densities for bottom type only. Data for all sites with the same bottom type were pooled, regardless of zone, and used to derive estimates of fish density.

RESULTS

During the 120 fish surveys of this assessment, a total of 7417 individual fish were counted from 35 families. The most abundant fish species were the bluehead wrasse (*Thalassoma bifasciatum*), slippery dick (*Halicoeres bivittatus*), ocean surgeonfish (*Acanthurus bahianus*), and blue tang (*Acanthurus coeruleus*), which together had the highest abundance values at hard-bottom sites (Table 1). Among the most frequently observed fish were the slippery dick (*H. bivittatus*: observed on 63% of all surveys), bluehead wrasse (*T. bifasciatum*: 48% of all surveys), striped parrotfish (*Scarus croicensis*: 38% of all surveys), blue tang and ocean surgeonfish (*A. coeruleus* and *A. bahianus*: each 37% of all surveys), bicolor damselfish (*Stegastes partitus*: 33% of all surveys), and French grunt (*Haemulon flavolineatum*: 31% of all surveys). Among the most rarely seen fish were the tiger grouper (*Mycteropera tigris*: 1% of all surveys), schoolmaster snapper (*Lutjanus apodus*: 1% of all surveys), peacock flounder (*Bothus lunatus*: 1% of all surveys), and Bermuda chub (*Kyphosus sectatrix*: 1% of all surveys). Differences in occurrence for most species were observed among zones, habitats, and strata (Table 1).

Overall species richness was 103; 62 species were found in both the lagoon and bank/shelf, eight species were found exclusively within the lagoon of the old BIRNM boundaries, and 33 were found exclusively on the bank/shelf within the expanded BIRNM boundaries. Of the 103 species observed, 39 were only found over hard-bottom, 11 were only over seagrass, three were found only over sand, 30 were found over all three habitats, 10 were only at hard-bottom and seagrass sites, seven were at hard-bottom and sand sites, and three were found only at sand and seagrass locations. Mean species richness varied significantly by stratum (Figure 3; χ^2 81.9, $p<0.0001$). The hard-bottom of the lagoon and bank/shelf had an interquartile range of 15 to 25 species per survey; this was significantly more than sand and seagrass sites, which had an interquartile range of between only one to seven species present. Species richness did not differ among sand and seagrass strata, whether in the lagoon or on the bank/shelf (Figure 3).

Species diversity was also significantly higher on hard-bottom strata compared with sand or seagrass strata (Figure 4; χ^2 75.8, $p<0.0001$). Species diversity did not differ among sand and seagrass strata, either in the lagoon or on the bank/shelf (Figure 4).

Mean density of fish differed significantly among strata (Figure 5; χ^2 79.5, $p<0.0001$). Highest fish densities were observed for the hard-bottom strata, with typical densities in excess of 100 fish per 100 m^2 survey. This was significantly higher than fish densities observed over sand and seagrass strata, which in many cases had fewer than 20 fish per 100 m^2 survey. There were no differences in fish densities among sand and seagrass strata, whether in the lagoon or on the bank/shelf (Figure 5).

The total area of different habitat types within the BIRNM was used to calculate an estimate of the total population size of fish within the old and new Monument boundaries (Table 2). The areas of sand and hard-bottom within the 2001 boundaries were higher than the areas encompassed by the 1975 boundaries by a factor of ten, whereas seagrass area was increased by a factor of seven. These calculations do not

Table 1. Species recorded during censuses. The upper value for each species denotes mean number per survey plus/minus standard error of the mean. The lower, italicized value denotes the proportion of surveys on which that species was observed. Trophic group codes: Z, zooplanktivores; SI, fish that feed on sessile invertebrates; P, piscivores; O, omnivores; MI/P, fish that feed on mobile invertebrates/piscivores; MI, fish that feed on mobile invertebrates; H, herbivores.

Species	Trophic group	Overall	Zone		Structure			Stratum					
			Bank/Shelf	Lagoon	Hard bottom	Sand	Seagrass	Bank/Shelf			Lagoon		
								hard bottom	sand	seagrass	hard bottom	sand	seagrass
Abudefduf	Z	0.07 ± 0.04	0.01 ± 0.01	0.15 ± 0.11	0.17 ± 0.11			0.04 ± 0.04			0.29 ± 0.21		
saxatilis		*0.03*	*0.01*	*0.06*	*0.08*	*0*	*0*	*0.04*	*0*	*0*	*0.13*	*0*	*0*
Abudefduf	Z	0.01 ± 0.01		0.02 ± 0.02	0.02 ± 0.02						0.04 ± 0.04		
taurus		*0.01*	*0*	*0.02*	*0.02*	*0*	*0*	*0*	*0*	*0*	*0.04*	*0*	*0*
Acanthurus	H	4.18 ± 1.19	2.67 ± 0.59	6.46 ± 2.82	8.44 ± 2.78	0.89 ± 0.47	1.81 ± 0.84	5.04 ± 1.16	1.13 ± 0.70	1.83 ± 0.98	11.83 ± 5.41	0.42 ± 0.19	1.75 ± 1.66
bahianus		*0.37*	*0.33*	*0.42*	*0.60*	*0.22*	*0.19*	*0.63*	*0.17*	*0.21*	*0.58*	*0.33*	*0.17*
Acanthurus	H	1.41 ± 0.33	1.17 ± 0.43	1.77 ± 0.54	3.25 ± 0.75	0.22 ± 0.17	0.14 ± 0.10	2.96 ± 1.18	0.33 ± 0.26	0.21 ± 0.15	3.54 ± 0.95		
chirurgus		*0.23*	*0.19*	*0.29*	*0.50*	*0.06*	*0.06*	*0.42*	*0.08*	*0.08*	*0.58*	*0*	*0*
Acanthurus	H	5.43 ± 1.58	2.65 ± 1.56	9.60 ± 3.09	13.54 ± 3.66	0.06 ± 0.04		7.96 ± 4.56			19.13 ± 5.58	0.17 ± 0.11	
coeruleus		*0.37*	*0.29*	*0.48*	*0.88*	*0.06*	*0*	*0.88*	*0*	*0*	*0.88*	*0.17*	*0*
Acentronura	MI	0.01 ± 0.01	0.01 ± 0.01				0.03 ± 0.03			0.04 ± 0.04			
dendritica		*0.01*	*0.01*	*0*	*0*	*0*	*0.03*	*0*	*0*	*0.04*	*0*	*0*	*0*
Amblycirrhitus	Z	0.02 ± 0.01	0.03 ± 0.02		0.04 ± 0.03			0.08 ± 0.06					
pinos		*0.02*	*0.03*	*0*	*0.04*	*0*	*0*	*0.08*	*0*	*0*	*0*	*0*	*0*
Apogon	Z	0.03 ± 0.03		0.06 ± 0.06	0.06 ± 0.06						0.13 ± 0.13		
aurolineatus		*0.01*	*0*	*0.02*	*0.02*	*0*	*0*	*0*	*0*	*0*	*0.04*	*0*	*0*
Aulostomus	P	0.14 ± 0.04	0.17 ± 0.06	0.10 ± 0.04	0.35 ± 0.09			0.50 ± 0.16			0.21 ± 0.08		
maculatus		*0.12*	*0.13*	*0.10*	*0.29*	*0*	*0*	*0.38*	*0*	*0*	*0.21*	*0*	*0*
Balistes vetula	MI	0.04 ± 0.03	0.07 ± 0.05		0.10 ± 0.07			0.21 ± 0.13					
		0.03	*0.04*	*0*	*0.06*	*0*	*0*	*0.13*	*0*	*0*	*0*	*0*	*0*
Bodianus rufus	MI	0.04 ± 0.02	0.07 ± 0.04		0.10 ± 0.05			0.21 ± 0.10					
		0.03	*0.06*	*0*	*0.08*	*0*	*0*	*0.17*	*0*	*0*	*0*	*0*	*0*
Bothus lunatus	P	0.01 ± 0.01		0.02 ± 0.02			0.03 ± 0.03						0.08 ± 0.08
		0.01	*0*	*0.02*	*0*	*0*	*0.03*	*0*	*0*	*0*	*0*	*0*	*0.08*
Cantherhines	SI	0.03 ± 0.02	0.06 ± 0.03		0.06 ± 0.05	0.03 ± 0.03		0.13 ± 0.09	0.04 ± 0.04				
pullus		*0.03*	*0.04*	*0*	*0.04*	*0.03*	*0*	*0.08*	*0.04*	*0*	*0*	*0*	*0*
Canthigaster	O	0.18 ± 0.06	0.28 ± 0.09	0.04 ± 0.03	0.38 ± 0.13	0.06 ± 0.06	0.06 ± 0.04	0.67 ± 0.25	0.08 ± 0.08	0.08 ± 0.06	0.08 ± 0.06		
rostrata		*0.12*	*0.17*	*0.04*	*0.23*	*0.03*	*0.06*	*0.38*	*0.04*	*0.08*	*0.08*	*0*	*0*
Caranx	P	0.04 ± 0.04	0.07 ± 0.07				0.14 ± 0.14			0.21 ± 0.21			
bartholomaei		*0.01*	*0.01*	*0*	*0*	*0*	*0.03*	*0*	*0*	*0.04*	*0*	*0*	*0*
Caranx crysos	P	0.14 ± 0.08	0.24 ± 0.13			0.31 ± 0.22	0.17 ± 0.14		0.46 ± 0.33	0.25 ± 0.21			
		0.03	*0.06*	*0*	*0*	*0.06*	*0.06*	*0*	*0.08*	*0.08*	*0*	*0*	*0*
Caranx hippos	P	0.01 ± 0.01	0.01 ± 0.01		0.02 ± 0.02			0.04 ± 0.04					
		0.01	*0.01*	*0*	*0.02*	*0*	*0*	*0.04*	*0*	*0*	*0*	*0*	*0*
Caranx ruber	P	0.48 ± 0.12	0.43 ± 0.18	0.56 ± 0.14	0.69 ± 0.19	0.19 ± 0.07	0.50 ± 0.31	0.50 ± 0.28	0.17 ± 0.08	0.63 ± 0.46	0.88 ± 0.25	0.25 ± 0.13	0.25 ± 0.13
		0.23	*0.14*	*0.38*	*0.33*	*0.19*	*0.14*	*0.17*	*0.17*	*0.08*	*0.50*	*0.25*	*0.25*
Chaetodon	SI	0.18 ± 0.06	0.28 ± 0.10	0.02 ± 0.02	0.42 ± 0.14	0.03 ± 0.03		0.79 ± 0.26	0.04 ± 0.04		0.04 ± 0.04		
capistratus		*0.09*	*0.14*	*0.02*	*0.21*	*0.03*	*0*	*0.38*	*0.04*	*0*	*0.04*	*0*	*0*
Chaetodon	SI	0.04 ± 0.03	0.03 ± 0.02	0.06 ± 0.06	0.06 ± 0.06	0.03 ± 0.03	0.03 ± 0.03		0.04 ± 0.04	0.04 ± 0.04	0.13 ± 0.13		
ocellatus		*0.03*	*0.03*	*0.02*	*0.02*	*0.03*	*0.03*	*0*	*0.04*	*0.04*	*0.04*	*0*	*0*

Chaetodon	SI	0.03 ± 0.02	0.03 ± 0.02	0.04 ± 0.04	0.06 ± 0.05	0.03 ± 0.03		0.04 ± 0.04	0.04 ± 0.04		0.08 ± 0.08						
striatus		*0.03*	*0.03*	*0.02*	*0.04*	*0.03*	*0*	*0.04*	*0.04*	*0*	*0.04*	*0*	*0*				
Chromis	Z	4.01 ± 1.38	6.68 ± 2.25		9.92 ± 3.28	0.03 ± 0.03	0.11 ± 0.11	19.83 ± 5.96	0.04 ± 0.04	0.17 ± 0.17							
cyanea		*0.12*	*0.19*	*0*	*0.25*	*0.03*	*0.03*	*0.50*	*0.04*	*0.04*	*0*	*0*	*0*				
Chromis	Z	0.15 ± 0.09	0.25 ± 0.15		0.38 ± 0.22			0.75 ± 0.43									
multilineata		*0.03*	*0.04*	*0*	*0.06*	*0*	*0*	*0.13*	*0*	*0*	*0*	*0*	*0*				
Clepticus	Z	0.60 ± 0.27	1.00 ± 0.44		1.50 ± 0.65			3.00 ± 1.24									
parrai		*0.05*	*0.08*	*0*	*0.13*	*0*	*0*	*0.25*	*0*	*0*	*0*	*0*	*0*				
Coryphopterus	O	0.43 ± 0.11	0.54 ± 0.17	0.25 ± 0.08	0.67 ± 0.23	0.31 ± 0.12	0.22 ± 0.11	1.04 ± 0.44	0.33 ± 0.18	0.25 ± 0.14	0.29 ± 0.11	0.25 ± 0.13	0.17 ± 0.17				
glaucofraenum		*0.22*	*0.22*	*0.21*	*0.27*	*0.22*	*0.14*	*0.29*	*0.21*	*0.17*	*0.25*	*0.25*	*0.08*				
Coryphopterus	Z	0.18 ± 0.18	0.29 ± 0.29		0.44 ± 0.44			0.88 ± 0.88									
personatus		*0.01*	*0.01*	*0*	*0.02*	*0*	*0*	*0.04*	*0*	*0*	*0*	*0*	*0*				
Cryptotomus	H	0.50 ± 0.16	0.72 ± 0.25	0.17 ± 0.13			1.67 ± 0.49			2.17 ± 0.67							
roseus		*0.13*	*0.18*	*0.04*	*0*	*0*	*0.42*	*0*	*0*	*0.54*	*0*	*0*	*0.17*				
Dasyatis	MI/P	0.09 ± 0.08	0.15 ± 0.14			0.03 ± 0.03	0.28 ± 0.28		0.04 ± 0.04	0.42 ± 0.42							
americana		*0.02*	*0.03*	*0*	*0*	*0.03*	*0.03*	*0*	*0.04*	*0.04*	*0*	*0*	*0*				
Decapterus	Z	0.24 ± 0.14	0.40 ± 0.24		0.02 ± 0.02	0.19 ± 0.14	0.58 ± 0.46	0.04 ± 0.04	0.29 ± 0.20	0.88 ± 0.69							
macarellus		*0.04*	*0.07*	*0*	*0.02*	*0.06*	*0.06*	*0.04*	*0.08*	*0.08*	*0*	*0*	*0*				
Diodon hystrix	MI	0.01 ± 0.01	0.01 ± 0.01			0.03 ± 0.03				0.04 ± 0.04							
		0.01	*0.01*	*0*	*0*	*0*	*0.03*	*0*	*0*	*0.04*	*0*	*0*	*0*				
Epinephelus	MI/P	0.06 ± 0.03	0.08 ± 0.04	0.02 ± 0.02	0.13 ± 0.06		0.03 ± 0.03	0.21 ± 0.12		0.04 ± 0.04	0.04 ± 0.04						
cruentatus		*0.04*	*0.06*	*0.02*	*0.08*	*0*	*0.03*	*0.13*	*0*	*0.04*	*0.04*	*0*	*0*				
Epinephelus	MI/P	0.45 ± 0.10	0.49 ± 0.14	0.40 ± 0.14	0.75 ± 0.18	0.47 ± 0.22	0.03 ± 0.03	0.71 ± 0.24	0.71 ± 0.33	0.04 ± 0.04	0.79 ± 0.26						
fulvus		*0.19*	*0.19*	*0.19*	*0.35*	*0.14*	*0.03*	*0.33*	*0.21*	*0.04*	*0.38*	*0*	*0*				
Epinephelus	MI/P	0.17 ± 0.04	0.24 ± 0.07	0.06 ± 0.04	0.27 ± 0.08	0.14 ± 0.08	0.06 ± 0.04	0.42 ± 0.15	0.21 ± 0.12	0.08 ± 0.06	0.13 ± 0.07						
guttatus		*0.13*	*0.18*	*0.06*	*0.23*	*0.08*	*0.06*	*0.33*	*0.13*	*0.08*	*0.13*	*0*	*0*				
Eucinostomus	MI	0.05 ± 0.04	0.08 ± 0.06			0.17 ± 0.12	0.00 ± 0.00		0.25 ± 0.18								
melanopterus		*0.02*	*0.03*	*0*	*0*	*0.06*	*0.00*	*0*	*0.08*	*0*	*0*	*0*	*0*				
Gerres cinereus	MI	0.13 ± 0.04	0.04 ± 0.02	0.25 ± 0.09	0.25 ± 0.09	0.06 ± 0.04	0.03 ± 0.03	0.08 ± 0.06	0.04 ± 0.04		0.42 ± 0.16	0.08 ± 0.08	0.08 ± 0.08				
		0.10	*0.04*	*0.19*	*0.19*	*0.06*	*0.03*	*0.08*	*0.04*	*0*	*0.29*	*0.08*	*0.08*				
Gnatholepis	O	0.03 ± 0.03	0.04 ± 0.04				0.08 ± 0.08			0.13 ± 0.13							
thompsoni		*0.01*	*0.01*	*0*	*0*	*0*	*0.03*	*0*	*0*	*0.04*	*0*	*0*	*0*				
Gobiosoma	O	0.02 ± 0.01	0.01 ± 0.01	0.02 ± 0.02	0.04 ± 0.03			0.04 ± 0.04			0.04 ± 0.04						
evelynae		*0.02*	*0.01*	*0.02*	*0.04*	*0*	*0*	*0.04*	*0*	*0*	*0.04*	*0*	*0*				
Gobiosoma	O	0.01 ± 0.01	0.01 ± 0.01				0.03 ± 0.03			0.04 ± 0.04							
genie		*0.01*	*0.01*	*0*	*0*	*0*	*0.03*	*0*	*0*	*0.04*	*0*	*0*	*0*				
Gramma loreto	Z	0.17 ± 0.13	0.28 ± 0.22		0.42 ± 0.33			0.83 ± 0.65									
		0.02	*0.03*	*0*	*0.04*	*0*	*0*	*0.08*	*0*	*0*	*0*	*0*	*0*				
Haemulon	MI	0.10 ± 0.07	0.07 ± 0.05	0.15 ± 0.15	0.21 ± 0.16		0.06 ± 0.06	0.13 ± 0.13		0.08 ± 0.08	0.29 ± 0.29						
aurolineatum		*0.03*	*0.03*	*0.02*	*0.04*	*0*	*0.03*	*0.04*	*0*	*0.04*	*0.04*	*0*	*0*				
Haemulon	MI	1.08 ± 0.29	0.61 ± 0.15	1.77 ± 0.68	2.52 ± 0.67	0.11 ± 0.07	0.11 ± 0.08	1.58 ± 0.37	0.08 ± 0.08	0.17 ± 0.12	3.46 ± 1.28	0.17 ± 0.11					
flavolineatum		*0.31*	*0.25*	*0.40*	*0.67*	*0.08*	*0.06*	*0.63*	*0.04*	*0.08*	*0.71*	*0.17*	*0*				
Haemulon	MI	0.04 ± 0.03	0.07 ± 0.06		0.02 ± 0.02		0.11 ± 0.11	0.04 ± 0.04		0.17 ± 0.17							
macrostomum		*0.02*	*0.03*	*0*	*0.02*	*0*	*0.03*	*0.04*	*0*	*0.04*	*0*	*0*	*0*				
Haemulon	MI	0.02 ± 0.01	0.01 ± 0.01	0.02 ± 0.02	0.04 ± 0.03			0.04 ± 0.04			0.04 ± 0.04						
plumieri		*0.02*	*0.01*	*0.02*	*0.04*	*0*	*0*	*0.04*	*0*	*0*	*0.04*	*0*	*0*				
Haemulon	MI	0.07 ± 0.03	0.01 ± 0.01	0.15 ± 0.06	0.17 ± 0.06			0.04 ± 0.04			0.29 ± 0.11						
sciurus		*0.06*	*0.01*	*0.13*	*0.15*	*0*	*0*	*0.04*	*0*	*0*	*0.25*	*0*	*0*				
Halichoeres	MI	8.19 ± 1.10	6.10 ± 1.06	11.33 ± 2.17	14.38 ± 2.19	4.39 ± 1.16	3.75 ± 1.13	8.79 ± 2.20	5.17 ± 1.71	4.33 ± 1.50	19.96 ± 3.47	2.83 ± 0.64	2.58 ± 1.64				
bivittatus		*0.63*	*0.54*	*0.77*	*0.75*	*0.64*	*0.47*	*0.63*	*0.46*	*0.54*	*0.88*	*1.00*	*0.33*				

Table 1. (*continued*)

Species	Trophic group	Overall	Zone		Structure			Stratum					
			Bank/Shelf	Lagoon	Hard bottom	Sand	Seagrass	Bank/Shelf			Lagoon		
								hard bottom	sand	seagrass	hard bottom	sand	seagrass
Halichoeres	MI	1.08 ± 0.25	1.42 ± 0.40	0.58 ± 0.18	2.54 ± 0.57	0.22 ± 0.11	0.00 ± 0.00	3.92 ± 1.04	0.33 ± 0.16		1.17 ± 0.31		
garnoti		*0.32*	*0.35*	*0.27*	*0.69*	*0.14*	*0.00*	*0.83*	*0.21*	*0*	*0.54*	*0*	*0*
Halichoeres	MI	0.77 ± 0.20	0.93 ± 0.31	0.52 ± 0.18	1.81 ± 0.46	0.08 ± 0.08	0.06 ± 0.06	2.67 ± 0.82	0.13 ± 0.13		0.96 ± 0.33		0.17 ± 0.17
maculipinna		*0.23*	*0.24*	*0.21*	*0.52*	*0.03*	*0.03*	*0.67*	*0.04*	*0*	*0.38*	*0*	*0.08*
Halichoeres	MI	0.21 ± 0.13	0.29 ± 0.20	0.08 ± 0.07	0.52 ± 0.31			0.88 ± 0.60			0.17 ± 0.13		
pictus		*0.04*	*0.04*	*0.04*	*0.10*	*0*	*0*	*0.13*	*0*	*0*	*0.08*	*0*	*0*
Halichoeres	MI	0.02 ± 0.02	0.03 ± 0.03				0.06 ± 0.06			0.08 ± 0.08			
poeyi		*0.01*	*0.01*	*0*	*0*	*0*	*0.03*	*0*	*0*	*0.04*	*0*	*0*	*0*
Halichoeres	MI	0.28 ± 0.07	0.18 ± 0.07	0.44 ± 0.13	0.69 ± 0.16		0.03 ± 0.03	0.50 ± 0.21		0.04 ± 0.04	0.88 ± 0.23		
radiatus		*0.16*	*0.11*	*0.23*	*0.38*	*0*	*0.03*	*0.29*	*0*	*0.04*	*0.46*	*0*	*0*
Heteroconger	Z	0.94 ± 0.94	1.57 ± 1.57			3.14 ± 3.14			4.71 ± 4.71				
halis		*0.01*	*0.01*	*0*	*0*	*0.03*	*0*	*0*	*0.04*	*0*	*0*	*0*	*0*
Holacanthus	SI	0.02 ± 0.01	0.03 ± 0.02		0.02 ± 0.02	0.03 ± 0.03		0.04 ± 0.04	0.04 ± 0.04				
tricolor		*0.02*	*0.03*	*0*	*0.02*	*0.03*	*0*	*0.04*	*0.04*	*0*	*0*	*0*	*0*
Holocentrus	MI	0.10 ± 0.04	0.13 ± 0.06	0.06 ± 0.04	0.17 ± 0.07	0.03 ± 0.03	0.08 ± 0.08	0.21 ± 0.12	0.04 ± 0.04	0.13 ± 0.13	0.13 ± 0.07		
adscensionis		*0.07*	*0.07*	*0.06*	*0.13*	*0.03*	*0.03*	*0.13*	*0.04*	*0.04*	*0.13*	*0*	*0*
Holocentrus	MI	0.02 ± 0.02	0.03 ± 0.03		0.04 ± 0.04			0.08 ± 0.08					
coruscus		*0.01*	*0.01*	*0*	*0.02*	*0*	*0*	*0.04*	*0*	*0*	*0*	*0*	*0*
Holocentrus	MI	0.35 ± 0.07	0.39 ± 0.11	0.29 ± 0.10	0.63 ± 0.14	0.19 ± 0.09	0.14 ± 0.11	0.71 ± 0.23	0.25 ± 0.12	0.21 ± 0.17	0.54 ± 0.18	0.08 ± 0.08	
rufus		*0.22*	*0.21*	*0.23*	*0.40*	*0.14*	*0.06*	*0.38*	*0.17*	*0.08*	*0.42*	*0.08*	*0*
Hypoplectrus	MI	0.07 ± 0.03	0.11 ± 0.05		0.17 ± 0.07			0.33 ± 0.13					
chlorurus		*0.05*	*0.08*	*0*	*0.13*	*0*	*0*	*0.25*	*0*	*0*	*0*	*0*	*0*
Hypoplectrus	MI	0.01 ± 0.01	0.01 ± 0.01		0.02 ± 0.02			0.04 ± 0.04					
nigricans		*0.01*	*0.01*	*0*	*0.02*	*0*	*0*	*0.04*	*0*	*0*	*0*	*0*	*0*
Hypoplectrus	MI	0.09 ± 0.04	0.15 ± 0.07		0.23 ± 0.10			0.46 ± 0.19					
puella		*0.04*	*0.07*	*0*	*0.10*	*0*	*0*	*0.21*	*0*	*0*	*0*	*0*	*0*
Ioglossus	Z	0.01 ± 0.01		0.02 ± 0.02	0.02 ± 0.02						0.04 ± 0.04		
helenae		*0.01*	*0*	*0.02*	*0.02*	*0*	*0*	*0*	*0*	*0*	*0.04*	*0*	*0*
Kyphosus	H	0.01 ± 0.01		0.02 ± 0.02	0.02 ± 0.02						0.04 ± 0.04		
sectatrix		*0.01*	*0*	*0.02*	*0.02*	*0*	*0*	*0*	*0*	*0*	*0.04*	*0*	*0*
Lactophrys	O	0.07 ± 0.03	0.10 ± 0.04	0.02 ± 0.02	0.15 ± 0.06	0.03 ± 0.03		0.25 ± 0.11	0.04 ± 0.04		0.04 ± 0.04		
triqueter		*0.06*	*0.08*	*0.02*	*0.13*	*0.03*	*0*	*0.21*	*0.04*	*0*	*0.04*	*0*	*0*
Lutjanus	MI/P	0.03 ± 0.02	0.01 ± 0.01	0.06 ± 0.04	0.04 ± 0.03	0.03 ± 0.03	0.03 ± 0.03			0.04 ± 0.04	0.08 ± 0.06	0.08 ± 0.08	
analis		*0.03*	*0.01*	*0.06*	*0.04*	*0.03*	*0.03*	*0*	*0*	*0.04*	*0.08*	*0.08*	*0*
Lutjanus	MI/P	0.01 ± 0.01	0.01 ± 0.01		0.02 ± 0.02			0.04 ± 0.04					
apodus		*0.01*	*0.01*	*0*	*0.02*	*0*	*0*	*0.04*	*0*	*0*	*0*	*0*	*0*
Lutjanus	MI/P	0.07 ± 0.05		0.17 ± 0.11	0.17 ± 0.11						0.33 ± 0.22		
griseus		*0.03*	*0*	*0.06*	*0.06*	*0*	*0*	*0*	*0*	*0*	*0.13*	*0*	*0*
Lutjanus	MI/P	0.10 ± 0.07	0.04 ± 0.02	0.19 ± 0.17	0.25 ± 0.17			0.13 ± 0.07			0.38 ± 0.33		
mahogani		*0.04*	*0.04*	*0.04*	*0.10*	*0*	*0*	*0.13*	*0*	*0*	*0.08*	*0*	*0*
Lutjanus	MI/P	0.04 ± 0.02	0.06 ± 0.03	0.02 ± 0.02	0.10 ± 0.05			0.17 ± 0.10			0.04 ± 0.04		
synagris		*0.03*	*0.04*	*0.02*	*0.08*	*0*	*0*	*0.13*	*0*	*0*	*0.04*	*0*	*0*

Malacanthus plumieri	MI	0.11 ± 0.05 *0.08*	0.15 ± 0.08 *0.10*	0.04 ± 0.03 *0.04*	0.19 ± 0.11 *0.10*	0.06 ± 0.04 *0.06*	0.06 ± 0.04 *0.06*	0.29 ± 0.21 *0.13*	0.08 ± 0.06 *0.08*	0.08 ± 0.06 *0.08*	0.08 ± 0.06 *0.08*	*0*	*0*
Malacoctenus macropus	O	0.03 ± 0.02 *0.03*	0.01 ± 0.01 *0.01*	0.06 ± 0.05 *0.04*	0.06 ± 0.05 *0.04*	*0*	0.03 ± 0.03 *0.03*	*0*	*0*	0.04 ± 0.04 *0.04*	0.13 ± 0.09 *0.08*	*0*	*0*
Malacoctenus triangulatus	O	0.01 ± 0.01 *0.01*	*0*	0.02 ± 0.02 *0.02*	0.02 ± 0.02 *0.02*	*0*	*0*	*0*	*0*	*0*	0.04 ± 0.04 *0.04*	*0*	*0*
Microspathodon chrysurus	H	0.33 ± 0.08 *0.16*	0.42 ± 0.13 *0.15*	0.21 ± 0.07 *0.17*	0.83 ± 0.19 *0.40*	*0*	*0*	1.25 ± 0.34 *0.46*	*0*	*0*	0.42 ± 0.13 *0.33*	*0*	*0*
Mulloidichthys martinicus	MI	0.42 ± 0.13 *0.15*	0.17 ± 0.08 *0.08*	N *0.25*	0.77 ± 0.27 *0.29*	0.22 ± 0.15 *0.08*	0.14 ± 0.14 *0.03*	0.25 ± 0.14 *0.17*	0.04 ± 0.04 *0.04*	0.21 ± 0.21 *0.04*	1.29 ± 0.50 *0.42*	0.58 ± 0.43 *0.17*	*0*
Mycteroperca tigris	P	0.01 ± 0.01 *0.01*	0.01 ± 0.01 *0.01*	*0*	0.02 ± 0.02 *0.02*	*0*	*0*	0.04 ± 0.04 *0.04*	*0*	*0*	*0*	*0*	*0*
Myripristis jacobus	Z	0.02 ± 0.02 *0.01*	0.03 ± 0.03 *0.01*	*0*	0.04 ± 0.04 *0.02*	*0*	*0*	0.08 ± 0.08 *0.04*	*0*	*0*	*0*	*0*	*0*
Ocyurus chrysurus	MI/P	0.47 ± 0.11 0.19	0.46 ± 0.14 0.21	0.48 ± 0.18 0.17	0.92 ± 0.22 0.40	0.06 ± 0.06 0.03	0.28 ± 0.19 0.08	1.13 ± 0.35 0.50	0.08 ± 0.08 0.04	0.17 ± 0.13 0.08	0.71 ± 0.25 0.29	0	0.50 ± 0.50 0.08
Ophioblennius atlanticus	O	0.04 ± 0.02 *0.03*	0.04 ± 0.03 *0.03*	0.04 ± 0.03 *0.04*	0.10 ± 0.05 *0.08*	*0*	*0*	0.13 ± 0.09 *0.08*	*0*	*0*	0.08 ± 0.06 *0.08*	*0*	*0*
Opistognathus aurifrons	Z	0.02 ± 0.02 *0.01*	0.03 ± 0.03 *0.01*	*0*	*0*	0.06 ± 0.06 *0.03*	*0*	*0*	0.08 ± 0.08 *0.04*	*0*	*0*	*0*	*0*
Paradiplogrammus bairdi	MI	0.02 ± 0.01 *0.02*	0.01 ± 0.01 *0.01*	0.02 ± 0.02 *0.02*	*0*	*0*	0.06 ± 0.04 *0.06*	*0*	*0*	0.04 ± 0.04 *0.04*	*0*	*0*	0.08 ± 0.08 *0.08*
Pomacanthus paru	SI	0.04 ± 0.02 *0.03*	0.06 ± 0.03 *0.04*	0.02 ± 0.02 *0.02*	0.06 ± 0.04 *0.06*	*0*	0.06 ± 0.06 *0.03*	0.08 ± 0.06 *0.08*	*0*	0.08 ± 0.08 *0.04*	0.04 ± 0.04 *0.04*	*0*	*0*
Pseudupeneus maculatus	MI	0.80 ± 0.25 *0.23*	1.15 ± 0.40 *0.32*	0.27 ± 0.19 *0.08*	0.40 ± 0.12 *0.25*	0.11 ± 0.05 *0.11*	2.03 ± 0.79 *0.31*	0.63 ± 0.21 *0.38*	0.17 ± 0.08 *0.17*	2.67 ± 1.12 *0.42*	0.17 ± 0.10 *0.13*	*0*	0.75 ± 0.75 *0.08*
Scarus coeruleus	H	0.09 ± 0.07 *0.02*	*0*	0.23 ± 0.17 *0.04*	0.23 ± 0.17 *0.04*	*0*	*0*	*0*	*0*	*0*	0.46 ± 0.33 *0.08*	*0*	*0*
Scarus croicensis	H	3.49 ± 0.56 *0.38*	2.54 ± 0.63 *0.29*	4.92 ± 1.02 *0.52*	8.67 ± 1.03 *0.90*	0.03 ± 0.03 *0.03*	0.06 ± 0.04 *0.06*	7.58 ± 1.43 *0.83*	*0*	0.04 ± 0.04 *0.04*	9.75 ± 1.48 *0.96*	0.08 ± 0.08 *0.08*	0.08 ± 0.08 *0.08*
Scarus taeniopterus	H	0.43 ± 0.14 *0.12*	0.63 ± 0.21 *0.17*	0.15 ± 0.11 *0.04*	1.08 ± 0.32 *0.29*	*0*	*0*	1.88 ± 0.56 *0.50*	*0*	*0*	0.29 ± 0.22 *0.08*	*0*	*0*
Scarus vetula	H	0.25 ± 0.07 *0.13*	0.14 ± 0.07 *0.07*	0.42 ± 0.15 *0.21*	0.63 ± 0.17 *0.31*	*0*	*0*	0.42 ± 0.20 *0.21*	*0*	*0*	0.83 ± 0.28 *0.42*	*0*	*0*
Scomberomorus regalis	P	0.02 ± 0.01 *0.02*	0.03 ± 0.02 *0.03*	*0*	*0*	*0*	0.06 ± 0.04 *0.06*	*0*	*0*	0.08 ± 0.06 *0.08*	*0*	*0*	*0*
Serranus baldwini	MI	0.06 ± 0.04 *0.03*	0.08 ± 0.06 *0.03*	0.02 ± 0.02 *0.02*	0.02 ± 0.02 *0.02*	*0*	0.17 ± 0.12 *0.06*	*0*	*0*	0.25 ± 0.18 *0.08*	0.04 ± 0.04 *0.04*	*0*	*0*
Serranus tigrinus	MI	0.45 ± 0.08 *0.26*	0.40 ± 0.09 *0.25*	0.52 ± 0.16 *0.27*	0.96 ± 0.18 *0.50*	0.17 ± 0.07 *0.14*	0.06 ± 0.04 *0.06*	0.96 ± 0.21 *0.54*	0.17 ± 0.10 *0.13*	0.08 ± 0.06 *0.08*	0.96 ± 0.29 *0.46*	0.17 ± 0.11 *0.17*	*0*
Sparisoma atomarium	H	0.46 ± 0.14 *0.13*	0.39 ± 0.14 *0.15*	0.56 ± 0.29 *0.10*	0.96 ± 0.33 *0.25*	0.03 ± 0.03 *0.03*	0.22 ± 0.13 *0.08*	0.79 ± 0.37 *0.29*	0.04 ± 0.04 *0.04*	0.33 ± 0.19 *0.13*	1.13 ± 0.56 *0.21*	*0*	*0*
Sparisoma aurofrenatum	H	1.59 ± 0.28 *0.34*	1.89 ± 0.44 *0.33*	1.15 ± 0.27 *0.35*	3.73 ± 0.58 *0.73*	0.19 ± 0.10 *0.11*	0.14 ± 0.11 *0.06*	5.21 ± 1.00 *0.79*	0.29 ± 0.15 *0.17*	0.17 ± 0.17 *0.04*	2.25 ± 0.43 *0.67*	*0*	0.08 ± 0.08 *0.08*
Sparisoma chrysopterum	H	0.13 ± 0.05 *0.07*	0.04 ± 0.03 *0.03*	0.27 ± 0.13 *0.13*	0.33 ± 0.13 *0.17*	*0*	*0*	0.13 ± 0.09 *0.08*	*0*	*0*	0.54 ± 0.24 *0.25*	*0*	
Sparisoma radians	H	0.48 ± 0.13 *0.15*	0.54 ± 0.19 *0.14*	0.38 ± 0.16 *0.17*	0.33 ± 0.14 *0.15*	*0*	1.14 ± 0.37 *0.31*	0.25 ± 0.21 *0.08*	*0*	1.38 ± 0.50 *0.33*	0.42 ± 0.19 *0.21*	*0*	0.67 ± 0.50 *0.25*
Sparisoma rubripinne	H	0.08 ± 0.04 *0.04*	0.06 ± 0.03 *0.04*	0.10 ± 0.07 *0.04*	0.19 ± 0.09 *0.10*	*0*	*0*	0.17 ± 0.10 *0.13*	*0*	*0*	0.21 ± 0.15 *0.08*	*0*	*0*

Table 1. (*continued*)

Species	Trophic group	Overall	Zone		Structure			Stratum					
			Bank/Shelf	Lagoon	Hard bottom	Sand	Seagrass	Bank/Shelf			Lagoon		
								hard bottom	sand	seagrass	hard bottom	sand	seagrass
Sparisoma	H	1.77 ± 0.28	1.33 ± 0.33	2.42 ± 0.49	4.42 ± 0.49			4.00 ± 0.72			4.83 ± 0.67		
viride		*0.33*	*0.25*	*0.46*	*0.83*	*0*	*0*	*0.75*	*0*	*0*	*0.92*	*0*	*0*
Sphoeroides	MI	0.02 ± 0.01	0.03 ± 0.02				0.06 ± 0.04			0.08 ± 0.06			
spengleri		*0.02*	*0.03*	*0*	*0*	*0*	*0.06*	*0*	*0*	*0.08*	*0*	*0*	*0*
Sphyraena	P	0.04 ± 0.02	0.03 ± 0.02	0.06 ± 0.04	0.02 ± 0.02	0.03 ± 0.03	0.08 ± 0.05	0.04 ± 0.04	0.04 ± 0.04				0.25 ± 0.13
barracuda		*0.04*	*0.03*	*0.06*	*0.02*	*0.03*	*0.08*	*0.04*	*0.04*	*0*	*0*	*0*	*0.25*
Stegastes	H	1.33 ± 0.28	0.65 ± 0.20	2.35 ± 0.61	3.31 ± 0.60		0.03 ± 0.03	1.92 ± 0.52		0.04 ± 0.04	4.71 ± 1.01		
diencaeus		*0.24*	*0.18*	*0.33*	*0.58*	*0*	*0.03*	*0.50*	*0*	*0.04*	*0.67*	*0*	*0*
Stegastes	H	0.40 ± 0.14	0.15 ± 0.09	0.77 ± 0.33	1.00 ± 0.35			0.46 ± 0.27			1.54 ± 0.63		
dorsopunicans		*0.09*	*0.04*	*0.17*	*0.23*	*0*	*0*	*0.13*	*0*	*0*	*0.33*	*0*	*0*
Stegastes	H	2.39 ± 0.49	0.76 ± 0.23	4.83 ± 1.08	5.63 ± 1.05	0.22 ± 0.10	0.25 ± 0.22	1.88 ± 0.53	0.08 ± 0.06	0.33 ± 0.33	9.38 ± 1.73	0.50 ± 0.26	0.08 ± 0.08
leucostictus		*0.34*	*0.21*	*0.54*	*0.69*	*0.17*	*0.06*	*0.50*	*0.08*	*0.04*	*0.88*	*0.33*	*0.08*
Stegastes	H	2.06 ± 0.39	2.71 ± 0.56	1.08 ± 0.49	3.50 ± 0.79	1.92 ± 0.66	0.28 ± 0.22	4.88 ± 1.21	2.88 ± 0.94	0.38 ± 0.33	2.13 ± 0.94		0.08 ± 0.08
partitus		*0.33*	*0.38*	*0.25*	*0.58*	*0.22*	*0.08*	*0.71*	*0.33*	*0.08*	*0.46*	*0*	*0.08*
Stegastes	H	0.97 ± 0.25	1.06 ± 0.37	0.83 ± 0.26	2.42 ± 0.56			3.17 ± 1.00			1.67 ± 0.47		
planifrons		*0.22*	*0.19*	*0.25*	*0.54*	*0*	*0*	*0.58*	*0*	*0*	*0.50*	*0*	*0*
Synodus	P	0.02 ± 0.01	0.01 ± 0.01	0.02 ± 0.02	0.02 ± 0.02		0.03 ± 0.03			0.04 ± 0.04	0.04 ± 0.04		
intermedius		*0.02*	*0.01*	*0.02*	*0.02*	*0*	*0.03*	*0*	*0*	*0.04*	*0.04*	*0*	*0*
Thalassoma	MI	8.37 ± 1.14	7.31 ± 1.52	9.96 ± 1.70	18.10 ± 1.93	3.44 ± 1.32	0.31 ± 0.31	16.79 ± 3.35	N	0.46 ± 0.46	19.42 ± 1.98	1.00 ± 0.74	
bifasciatum		*0.48*	*0.42*	*0.58*	*0.94*	*0.33*	*0.03*	*0.88*	*0.33*	*0*	*1.00*	*0.33*	*0*
Xyrichthys	Z	0.78 ± 0.24	1.08 ± 0.38	0.33 ± 0.16	0.04 ± 0.04	1.75 ± 0.62	0.81 ± 0.46	0.08 ± 0.08	2.33 ± 0.88	0.83 ± 0.67		0.58 ± 0.50	0.75 ± 0.39
martinicensis		*0.17*	*0.19*	*0.13*	*0.02*	*0.31*	*0.22*	*0.04*	*0.38*	*0.17*	*0*	*0.17*	*0.33*
Xyrichthys	Z	0.27 ± 0.13	0.28 ± 0.20	0.25 ± 0.12		0.50 ± 0.37	0.39 ± 0.23		0.54 ± 0.54	0.29 ± 0.29		0.42 ± 0.29	0.58 ± 0.36
splendens		*0.06*	*0.03*	*0.10*	*0*	*0.08*	*0.11*	*0*	*0.04*	*0.04*	*0*	*0.17*	*0.25*

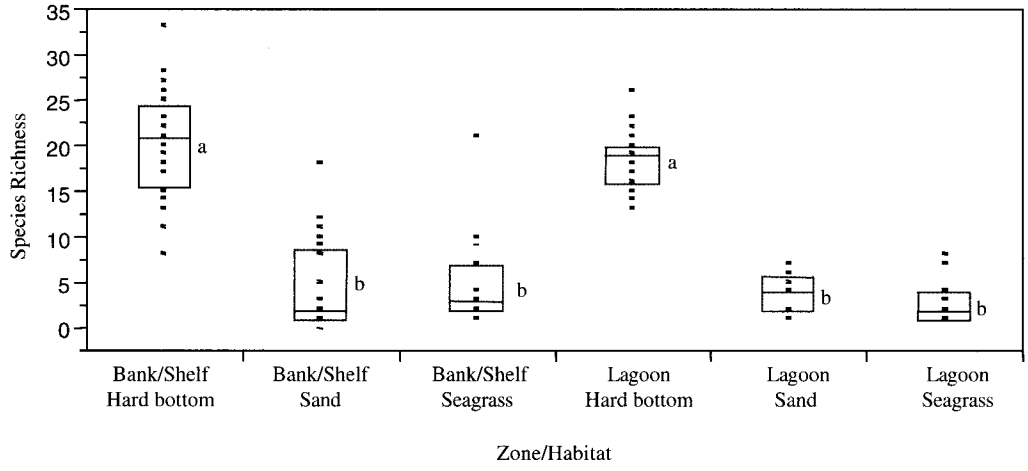

Figure 3. Species richness by stratum. Actual values for individual survey sites are plotted as points, boxes denote interquartile range, and the horizontal line through each box denotes the median for each group. Groups with the same letter are not significantly different from one another ($\alpha = 0.05$).

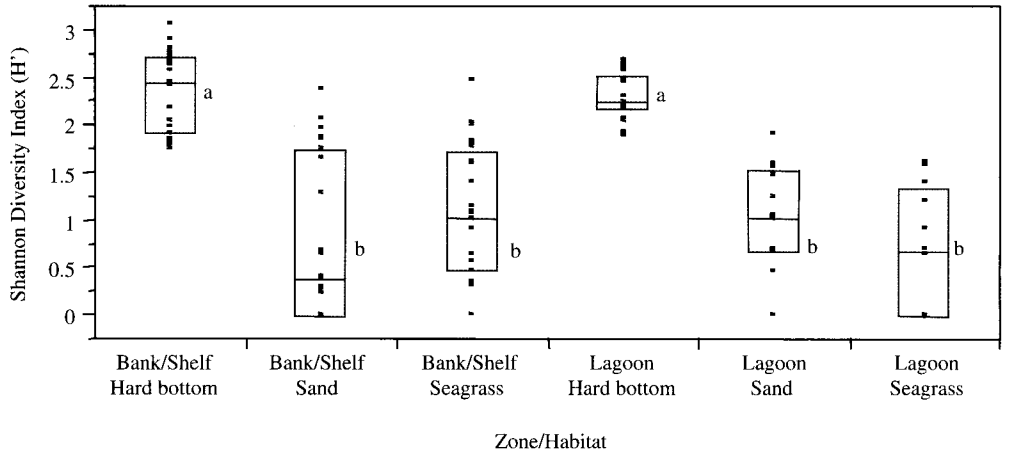

Figure 4. Shannon diversity index by stratum. Actual values are plotted as points, boxes denote interquartile range, and the horizontal line through each box denotes the median for each group. Groups with the same letter are not significantly different from one another ($\alpha = 0.05$).

include the very large area of extremely deep water that is now included in the BIRNM but for which no benthic maps or fish survey data are available (Figure 1). Applying values of fish density (Figure 5) to the measurable habitat area indicated that the estimated fish population size within the BIRNM increased from approximately 2.6 million to 24 million individuals with the expansion of the BIRNM boundaries (Table 2).

Examination of trophic ratios indicated that herbivorous fish and those that feed on mobile invertebrates dominated the assemblages of all strata. In lagoon hard-bottom sites, those two feeding modes made up an average of over 90% of all fish seen (Figure 6). The next most abundant feeding mode in nearly all strata was zooplanktivory, even though fish of this feeding mode generally made up a smaller proportion

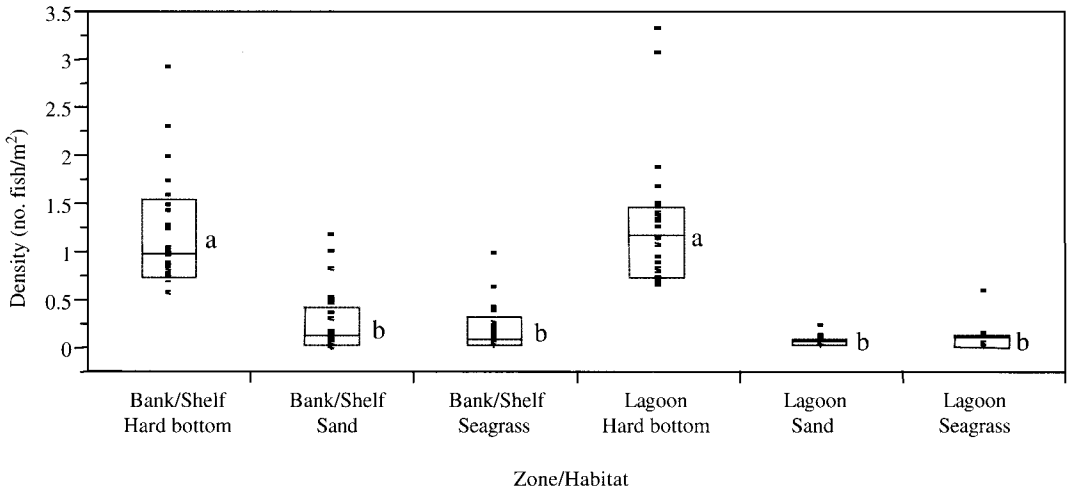

Figure 5. Density of fish by stratum. Actual values for individual survey sites are plotted as points, boxes denote interquartile range, and the horizontal line through each box denotes the median for each group. Groups with the same letter are not significantly different from one another ($\alpha = 0.05$).

Table 2. Area of habitat types and estimated size of fish population within 1961 and 2001 park boundaries

Habitat type	Habitat area (m^2)	Fish density by habitat (m^{-2})	Fish population by habitat	Total estimated population
1975 boundary				
Sand	293 000	0.20	58 600	
Seagrass	474 000	0.17	80 580	2 612 560
Hard bottom	1 963 000	1.26	24 73 380	
2001 boundary				
Sand	2 696 000	0.20	5 39 200	
Seagrass	2 892 000	0.17	4 91 640	24 085 060
Hard bottom	18 297 000	1.26	23 054 220	

of the fish assemblage in the lagoon relative to the bank/shelf and were nearly absent from lagoon hard-bottom sites.

Hierarchical clustering of strata based on the species present at each site revealed that the most similar species assemblages occurred between the two hard-bottom strata. Among the other four spatial strata, seagrass sites on the bank/shelf had a species assemblage different than that of seagrass in the lagoon and both sand strata. Finally, sand and seagrass in the lagoon had species assemblages more similar to each other in composition than they were to the assemblage on the bank/shelf sand (Figure 7).

PCA of spatial strata based on frequency of occurrence of each species revealed similar results. Two principal components explained 54% and 24% of the variations in these data. The remaining four components explained between 1 and 7% of the variation. Therefore, only the first two factor loadings were evaluated further. Along factor one there was clear differentiation between species associated with hard-bottom versus soft-bottom (sand and seagrass) (Figure 8). The second principal component explained much less of the pattern in the data but further separated the species into those found primarily in the three main habitat types.

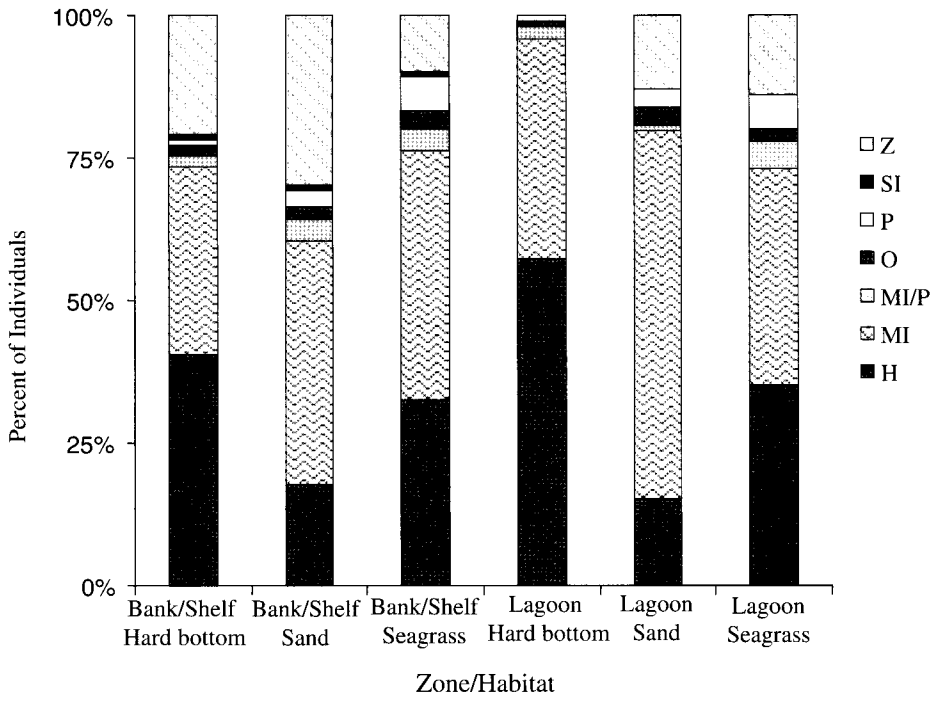

Figure 6. Ratio of the number of individuals in feeding guilds by spatial strata (Z: zooplanktivores; SI: fish that feed on sessile invertebrates; P: piscivores; O: omnivores; MI/P: fish that feed on mobile invertebrates/piscivores; MI: fish that feed on mobile invertebrates; H: herbivores).

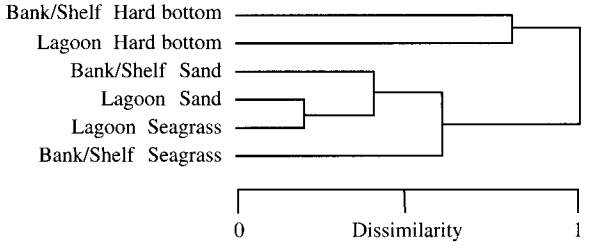

Figure 7. Hierarchical clustering of spatial strata by frequency of species occurrence using ward's minimum-variance method.

DISCUSSION

This study provides a baseline assessment of the fish biodiversity of the tropical marine ecosystem of the BIRNM, a no-take marine reserve. Several consistent patterns in fish community structure in relation to different strata were observed using multiple metrics and statistics. Hard-bottom substrates in both the lagoon and bank/shelf had similarly high levels of mean fish density, species richness, and diversity. Also, sand and seagrass areas, regardless of shelf position, had similar values for these three metrics, although they were significantly lower than values for hard-bottom substrates. No significant differences in mean fish

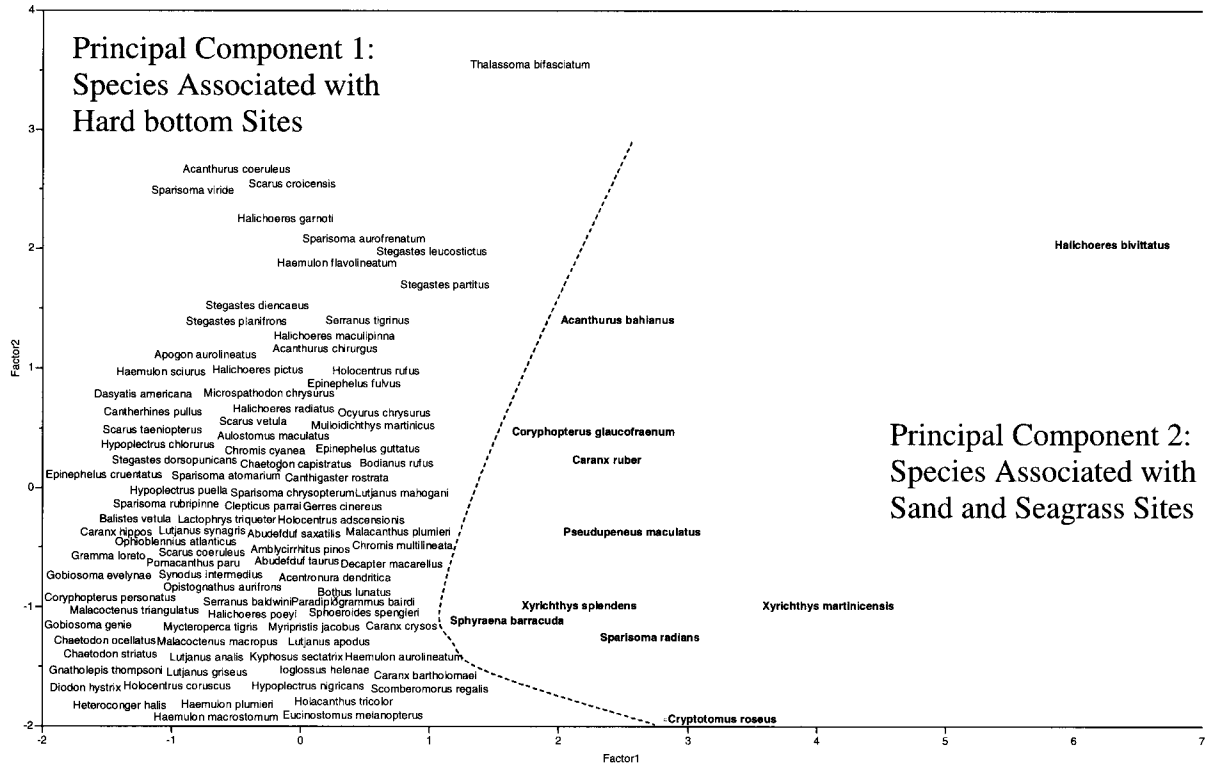

Figure 8. Factor Plot of PCA. Species to the left of the dotted line denote those within principal component one and are typical of coral reef sites. Species to the right denote those within principal component two and are typical of sand and seagrass sites.

density, species richness, or diversity were observed for areas having the same bottom type but occurring in different zones, indicating that bottom type is a more dominant factor than shelf position in determining the fish assemblage of a given area.

PCA and cluster analysis also identified similar patterns. These techniques are fundamentally different than the metrics discussed above, because they take into account the particular species associated with each stratum. For example, species richness assigns the same value for two survey sites, each with the same number of species, even though none of the species is common to both sites. PCA and cluster analysis take into account the differences in component species. Hard-bottom strata not only clustered separately from sand and lagoon strata but also fell into a similar pattern in PCA, again suggesting that bottom type exerted a greater influence on species assemblages than did position on the shelf.

The classification of fish into specific feeding guilds allowed comparison of trophic ratios among strata. Herbivores dominated most strata except for sand. Members of this feeding guild no doubt find ample forage not only in seagrass and macroalgal beds but also on the many species of algae that colonize the large areas of dead elkhorn coral, *A. palmata*, on the reefs of this region.

Shelf position did, however, play an important role in the distribution of fishes in the zooplanktivorous guild. Fewer fish with this feeding mode were found in the lagoon than on the bank/shelf, even when comparisons were made between sites having the same bottom type. In fact, almost no zooplanktivorous fish were observed on hard-bottom sites within the lagoon, whereas zooplanktivores comprised 20% of the individuals on hard-bottom sites on the bank/shelf. This could be explained by the dependence of these fish on water currents to carry suitable food items within reach. Currents are generally less intense within the

low-energy environment of the lagoon, which is insulated by the emergent reef from the stronger currents on the bank/shelf. The reduced volume of water crossing lagoon habitats may not provide a suitable forage base of drifting plankton to support large numbers or a diversity of fish in the zooplanktivorous trophic group relative to other feeding modes. Indeed, of the 33 species found exclusively on the bank/shelf, nearly one-third were in the zooplanktivorous guild.

The recent expansion of the BIRNM resulted in a 10-fold increase in the estimated population size of fish within its boundaries. An increase in species richness probably also occurred, since the expanded BIRNM boundaries now include a very large area of bank/shelf habitat whereas the 1961 boundaries of the BIRNM included the lagoon and only a very small area of bank/shelf. These additions represent enhancements to the biodiversity, population size, and habitat area of the ecosystem that is now under federal protection. It must be noted, however, that even more dramatic gains in species richness, population size, and habitat diversity have no doubt occurred but could not be measured by the scuba-based methods used in this study. In addition to under-sampling cryptic species at scuba depths, much of the acreage gained during the expansion of the BIRNM is in extremely deep water (200–900 m), well beyond the limits of both the aerial photographs used to create the benthic maps and the scuba census techniques used (Figure 1). Expanding this assessment to include cryptic fauna and the fish assemblages associated with the pelagic and deep-water habitats is needed to obtain a complete understanding of the biodiversity and ecosystem dynamics of this area.

The estimates of population size within the BIRNM boundaries generated here are crude but provide a useful initial estimate of Monument resources. The procedure used could be applied to individual species by using the density estimates provided in Table I to examine changes in community composition or fish abundance in the reserve over time. This approach, useful for making generalizations, does not take into account landscape-scale processes that are probably responsible for much of the variation that we observed in fish assemblages within strata. For example, Kendall *et al.* (2003) recently found that the distribution of juvenile French grunt (*H. flavolineatum*) depends not only on the specific habitat type over which surveys are conducted but also on the area of and distance to nearby sand and seagrass habitats. Fine-scale measures of habitat quality are not considered in this assessment either, but they obviously play a major role in determining the species assemblage of any given location (Kaufman and Ebersole, 1984). A similar assessment could be conducted using the 26 discrete categories in the original benthic maps rather than just the three general categories used here. Clearly, examining both broader and finer scales for the determinants of assemblage structure is required to obtain a more comprehensive understanding of the biogeography of the region.

It should also be emphasized that this assessment is based on daytime surveys only. The species assemblages of all the spatial strata will undergo changes as fish that utilize daytime refuges emerge from concealment and engage in night-time activities across habitat boundaries. The species richness, diversity, and overall abundance of fish probably achieve a more equitable distribution among the three major bottom types (sand, seagrass, and hard-bottom) at night, since several fish species disperse away from the diverse and dense reef community to feed solitarily over sand and seagrass habitats each evening (Helfman *et al.*, 1982; Burke, 1995). Another important caveat is that the logistics demanded that all surveys be conducted in February 2001. As a result, seasonal and interannual variations inherent to marine ecosystems were not evaluated with this study. These important aspects of community change will be addressed using the data collected subsequent to this study as part of the newly initiated long-term monitoring activities within the BIRNM.

When the BIRNM was established in 1961 its coral reef formations and associated habitats were identified as 'one of the finest marine gardens in the Caribbean Sea' (Presidential Proclamation 3443, 1962), despite a lack of quantitative data at that time. Enlarging the Monument in 2001 brought into protection many additional habitats not included in the initial boundary, such as nearby coral reefs, seagrass beds, sand areas, algal plains, shelf edges, and other habitats (Presidential Proclamation 7392, 2001), that are

inextricably linked in tropical marine landscapes. This assessment provides a timely quantification of many of these habitats and their associated biota.

The results of this study are useful both for local management at the BIRNM and for guiding selection of other marine protected areas in the region. Within the BIRNM, areas of particular concern can now be identified for enhanced protection, sites for fine-scale monitoring can be selected more appropriately, and damage assessment following natural or anthropogenic impacts can become quantitative. Regionally, this assessment places the BIRNM into context with an emerging network of marine reserves on adjacent islands and throughout the Caribbean (Lubchenco *et al.*, 2003). Given similar assessments in those reserves, the existing network can be examined for gaps in coverage and additional reserve sites considered more judiciously. In addition, given the ongoing debate regarding the optimal size and characteristics for marine reserves (Shanks *et al.*, 2003), this assessment provides an additional data point for meta-analysis or studies of reserve function that include comparison among many sites.

Over the 40 years since the BIRNM was originally designated, dramatic changes have taken place on the reef ecosystems of this region due to over-fishing and other factors (Rogers and Beets, 2001). White Band Disease and coral bleaching decimated elkhorn coral, *A. palmata*, colonies in the late 1970s and 1980s, which once dominated reef formations around Buck Island (Gladfelter, 1982), and without doubt impacted local fish assemblages (Lirman, 1999). In addition, the widespread die off of the once common sea urchin, *Diadema antillarum*, in 1984 altered the trophic balance of the reef ecosystem in the region (Lessons *et al.*, 1984). Unfortunately, since no baseline assessments of reef fish biodiversity and community structure are available for Buck Island prior to these events, scientists and managers can now only infer or speculate on the resulting changes to the reef fish community. With this study, the baseline condition of the fish community, which has been sliding unquantified for decades, has finally been assessed.

Perhaps the most important additional element of this assessment that is required is the collection of similar data for areas outside the marine reserve. Only by establishing baseline measures of assemblage structure outside of the marine reserve can the effects of the reserve be placed in their wider ecological context.

ACKNOWLEDGEMENTS

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